DESCRIPTION OF *ALETHOPTERIS* FROM THE WILLIAMSON #3 MINE, LUCAS COUNTY, IOWA: ANATOMICAL VARIATION, DIVERSITY, PALEOECOLOGY

A Thesis

by

ELIZABETH DUNBAR JONES SLONE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2003

Major Subject: Geology

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Approved as to style and content by:

Anne Raymond (Chair of Committee)	Thomas E. Yancey (Member)
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ABSTRACT

Description of *Alethopteris* from the Williamson #3 Mine, Lucas County, Iowa:

Anatomical Variation, Diversity, Paleoecology. (August 2003)

Elizabeth Dunbar Jones Slone, B.S., Auburn University

Chair of Advisory Committee: Dr. Anne Raymond

For more than 100 years, Pennsylvanian permineralized peats have been studied for their exceptionally preserved plant remains. Late Atokan-early Desmoinesian coal balls from the Williamson # 3 deposit in south-central Iowa were preserved by the permineralization of soluble carbonate into pores in the peat and plant cells creating carbonate nodules. These nodules, referred to as coal balls, protect the plant remains from the compaction associated with coal allowing for the analysis of anatomically preserved plants from Pennsylvanian.

The Williamson #3 deposit is unusual because it is dominated by a diverse assemblage of gymnosperms. Other deposits of similar age in Iowa are dominated by a mixture of cordaitalean gymnosperms, tree-ferns, and medullosan gymnosperms; while, other North American deposits are dominated by lycopsids with tree-ferns and seed-ferns as the subdominant vegetation. Because vegetation types differ with environment, analysis of the *Alethopteris* pinnules from the Williamson #3 Mine provides insight into the ecology of a peat-producing swamp during the Pennsylvanian, and allows for the comparison of this deposit to others in North America.

The focus of this study is the description of a distinct morphotype of *Alethopteris* from the Williamson #3 Mine. *Alethopteris* pinnules described from other mines were used to compile a traits list and compare measured and descriptive characteristics. The objective of this study is to gain a better understanding of changes in swamp vegetation during the Pennsylvanian, and the effect of environmental variation on the dominant vegetation in peat swamps.

ACKNOWLEDGMENTS

This study was possible due to specimen loans from the Harvard University Botanical Museum. The author would like to thank the members of this thesis committee including Dr. Anne Raymond, Dr. Tom Yancey, and Dr. Merrill Sweet. The author is grateful for the research material and support provided Suzanne Costanza and Alicia Lesnikowska. The author would also like to express thanks to Bo Slone, family, and friends for the love and emotional support to complete this project.

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INTRODUCTION

Pennsylvanian permineralized peats provide a source of anatomical information about fossil plants that is unique in the 400 million year history of vascular plants. Peat permineralization occurs when soluble carbonate, silicate, or iron sulfide compounds precipitate in pores and plant cells to form a rigid rock matrix supporting delicate plant tissues (Stewart and Rothwell, 1993). The features produced, referred to as coal balls, occur as scattered nodules or horizontal mineralized zones within the coal (Anderson et al., 1981). Coal balls are significant in understanding the histology of Pennsylvanian plants, because they form prior to coalification and protect plant material from the compaction associated with coal formation (Stopes and Watson, 1908; Behrensmeyer and Hook, 1992). As a result, detailed anatomical features of leaves, stems, reproductive structures, and roots can be observed. Most studies of Late Paleozoic foliage rely on the morphological features gathered from coalified compressions found in shales associated with coals. While these studies provide important information on leaf shape, venation, and stomatal characteristics, microscopic examination of permineralized macrodetritus provides additional insight into plant evolution and paleoecology. The present study focuses on anatomically preserved *Alethopteris* pinnules from the permineralized peat of the Williamson #3 Mine in Lucas County, Iowa (Fig. 1) in comparison to *Alethopteris* foliage of other North American mines (Fig. 2, 3). The objective is to gain insight into the ecology and seed-fern diversity of the Williamson #3 Coal, and to better understand changes in the swamp vegetation during the Pennsylvanian (Appendix A).

The Pennsylvanian marks a time of major paleotropical coal deposition that can be attributed to paleogeographic and climatic changes associated with Southern Hemisphere glaciation, and the collision of Gondwana and Euramerica, which began in the Mississippian (middle Visean: Lefort and Van der Voo, 1981) and continued into the Pennsylvanian (Raymond, 1996). Although the link between glaciation and paleotropical coal deposition may seem enigmatic, Ziegler et al. (1987) suggested that modern ever-wet

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This thesis follows the style of Review of Palaeobotany and Palynology.

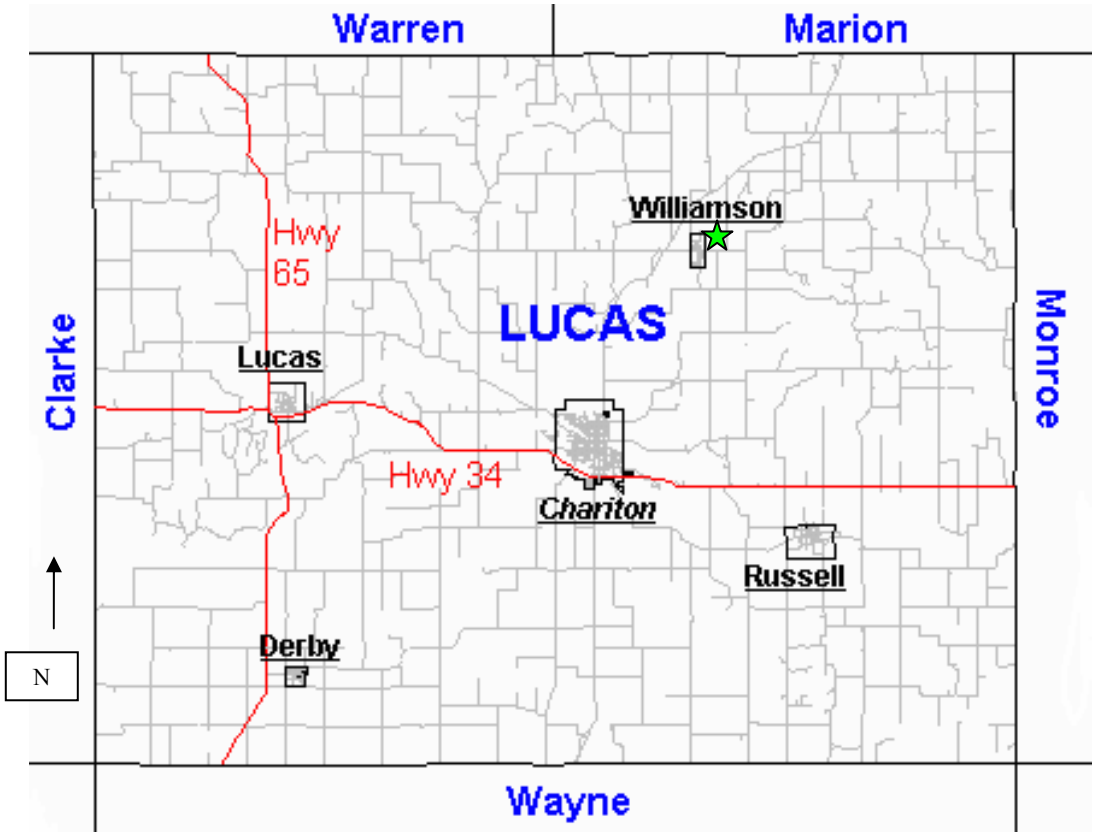


Fig. 1. Map of Lucus County, Iowa with the green star marking the approximate location of the Williamson #3 Mine. Modified from http//www.lucasco.net/cityhall

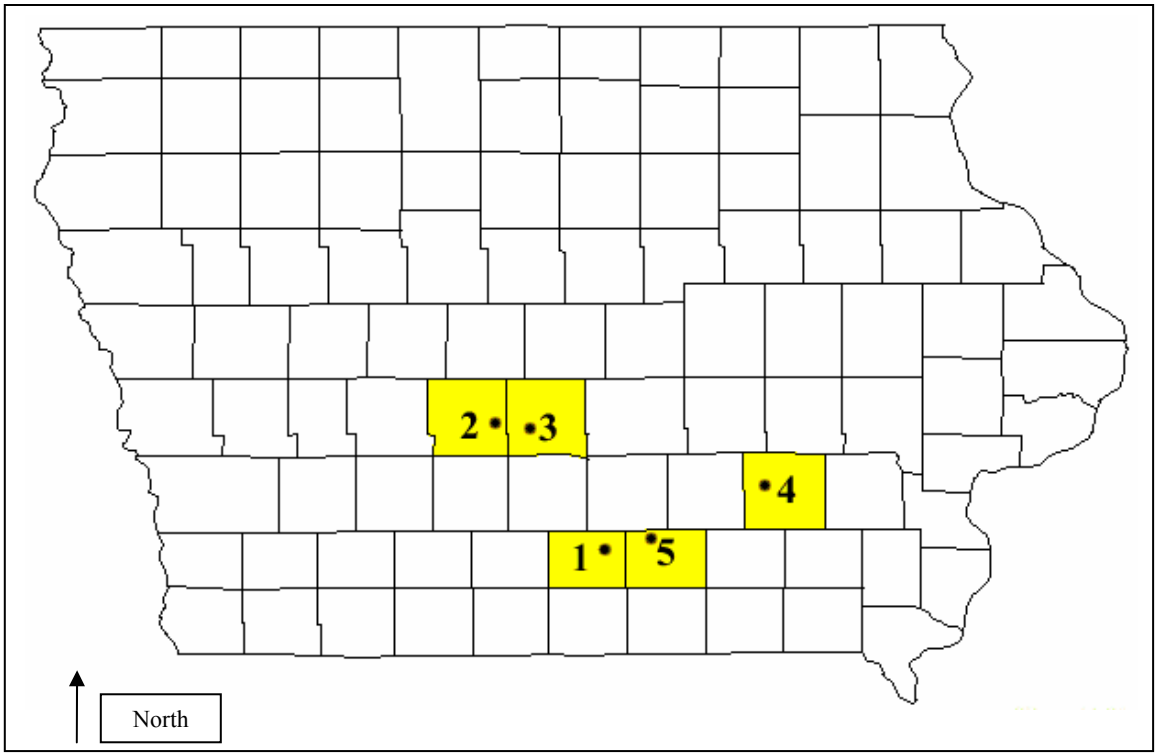


Fig. 2. Map of Iowa showing the approximate locations of important mines. Key: (1) Williamson #3 Mine, Lucas County; (2) Shuler Mine, Dallas County; (3) Urbandale Mine, Polk County; (4) What Cheer Clay Products Mine, Keokuk County; (5) Weldon Mine, Lovilia, Monroe County.

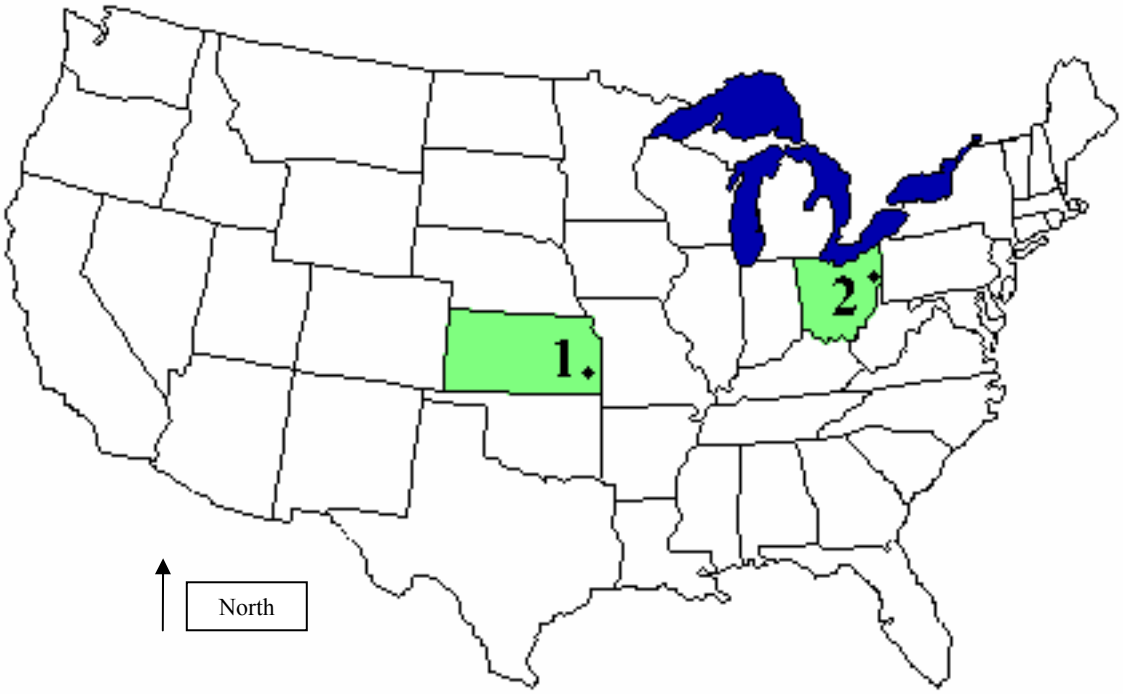


Fig. 3. Locations of other North American mines from which *Alethopteris* has been described. Key: (1) West Mineral, Kansas; (2) Steubenville, Ohio.

equatorial climates are dependent on the presence of polar glaciers. In both the Late Tertiary and the Late Mississippian – Early Pennsylvanian,"migrational and evolutionary patterns of marine invertebrates during intervals of glacial onset suggest that polar glaciers also cause equatorial warming" (Raymond, 1996).

During the Middle and Late Pennsylvanian, most of the continents had collided to form the pole - to - pole land landmass of Pangea (Ziegler et al., 1981; Blakey, 2003 (Fig. 4)). North America during this time was positioned such that the Appalachian coalfield had an approximate east-west orientation along the equatorial zone and was close to, if not connected to, the European continent (Schopf, 1975). Coal and peat-accumulating swamps extended from the Western and Eastern Interior Basins in the mid-continent region of North America to the Appalachian Basin, and across the Canadian Maritime Provinces, into Europe and South China (Chaloner and Meyen, 1973; Ziegler et al. 1981). Each of these regions lay near the equator and experienced tropical or subtropical climates (Raymond, 1996; Ziegler et al., 1981). In Euramerica, the lack of seasonality associated with tropical environments is demonstrated by the absence of growth rings in Pennsylvanian-age petrified wood (Chaloner and Meyen, 1973). Epicontinential seas were extensive and bordered by barrier bars, estuaries, tidal flats, and "vast areas of interior swamps at elevations little more than a few feet above tide level" (Schopf, 1975).

DiMichele and Phillips (1995) depicted Middle to Late Desmoinesian swamp communities as relatively persistent, with species turnover occurring mostly within habitats. Replacement species came from the same genus or closely related genera and were morphologically similar. Distinct plant communities separated by substrate types, abundance of water, and nutrient levels composed these vast lowland peat-forming mires (DiMichele and Phillips, 1996b).

In a series of contributions, DiMichele and Phillips (1995, 1996a, 1996b) discussed five recurring assemblages, or communities, which inhabited an environmental gradient from ever-wet to seasonally-drained substrates. Monocarpic lycopsids such as *Lepidophloios hallii* dominated communities growing in areas inundated with standing water for long periods. These had low species richness and low percentages of ground cover and free sporing plants. Communities dominated by the polycarpic lycopsids such as *Diaphorodendron scleroticum* with various subdominants (pteridosperms, lycopsids, tree ferns, and ground

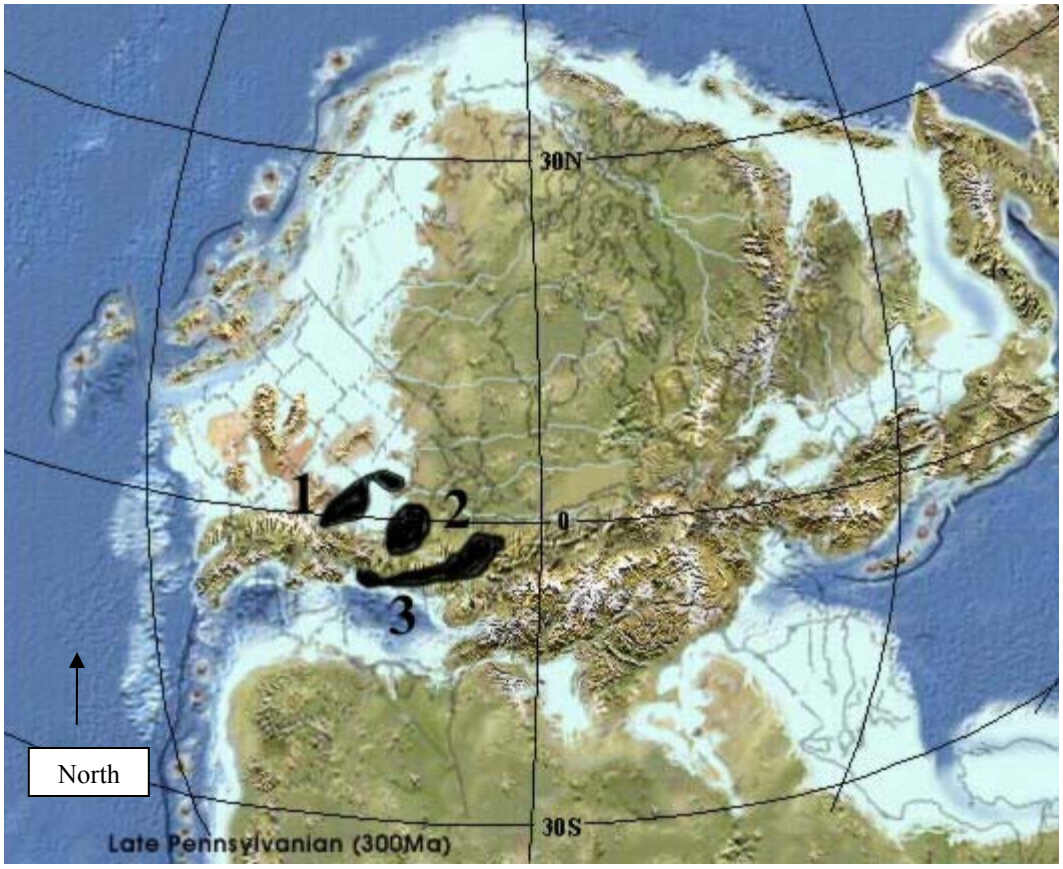


Fig. 4. Paleogeography of North America during the Late Pennsylvanian modified from Blakey, 2003. Key: (1) Western Interior Basin; (2) Eastern Interior Basin; (3) Appalachian Coal Region.

cover) inhabited wet, but irregularly flooded areas of the swamp. *Medullosa* pteridosperm species and/or the small lycopsid *Paralycopodites brevifolius* dominated communities growing on transitional peats (i.e. the ecotonal environment between water-logged clastic and peat substrates). Peats derived from these communities are enriched in clastics and fusain (mineralized charcoal) and also contain tree ferns, calamites, and abundant ground cover. The *Sigillaria* community is thought to have grown on a periodically dry peat surface. The final community, the *Chaloneria* and *Sphenophyllum* community, has been compared to a modern-day marsh (DiMichele and Phillips, 1996a; DiMichele and Phillips, 1996b). Thus, swamps of this time are characterized by flooded, low nutrient, organic rich substrates in the wettest parts of the lowlands, a transitional environment that is wet but only occasionally flooded, and less waterlogged parts of the lowland that "experienced periodic moisture limitations" (DiMichele et al., 1985).

Three major vegetational changes occurred in peat-accumulating swamps during the Middle and Late Pennsylvanian (Appendix B). Late Atokan and early Desmoinesian, peat-accumulating communities in the Western Interior Basin and the Appalachian Basin were generally dominated by *Cordaites*, with lycopsids or tree ferns as subdominant components of the swamp (Phillips, et al., 1985; Raymond, 1988; Slone et al., 2001). In contrast, swamps of equivalent age in the Eastern Interior Basin were dominated by lycopsids and tree ferns (Phillips et al., 1985). The abundance of *Cordaites* in late Atokan – early Desmoinesian swamps from the Western Interior Basin has been attributed both to the presences of salt water (Cridland, 1964; Raymond, 1988) and to decreased water availability (Phillips and Peppers, 1984; Phillips et al., 1985). A better understanding of the depositional environment of cordaite-dominated deposits from the Western Interior Basin suggests that cordaite dominance results from seasonal drying rather than the presence of salt water (Raymond et al., 2001)

The Williamson #3 deposit is unusual because it is dominated by a diverse assemblage of seed plants (both *Cordaites* and medullosan seed-ferns) with only a small percent of the biomass attributed to lycopsids (Phillips et al., 1985; Raymond, 1988; Raymond et al., 2001; Slone et al., 2001). Information about the paleogeographic position of Iowa during the Desmoinesian, in conjunction with the abundance of pteridosperms, suggests that the Williamson # 3 swamp experienced increased seasonality associated with the first relatively dry interval in the early Desmoinesian described by Phillips and Peppers (1984) and Phillips et al. (1985). In addition, a decrease in water availability may also be attributed to a rise in the input of siliciclastics into the swamps from more upland regions to the northeast causing soils to better drained during the dry seasons (White, 1931).

By the middle and late Desmoinesian, the frequency of tree-fern and seed-fern dominated communities in peat-accumulating swamps of the Western Interior Basin decreased. Cordaitalean-dominated communities from this interval persisted only in a few coals: the Mineral-Fleming Coals in Kansas and the Lovilia coal deposit in Iowa (Phillips et al., 1985; Brotzman, 1974). Despite the presence of cordaitalean-dominated communities, lycopsids dominated most middle to late Desmoinesian coals. The Eastern Interior Basin and Appalachian Basin experienced a more stable environment with lycopsids remaining the dominant plant type with seed-ferns and tree-ferns as subdominants.

A more catastrophic event followed at the Desmoinesian-Missourian boundary when the Desmoinesian glacial maximum came to an abrupt end, causing regional drying in western Eurameria (DiMichele and Phillips, 1996b). In response, tree-fern and seed-fern communities replaced the lycopsid communities within the peat swamps of North America and Europe (Phillips et al., 1985). This shift in vegetation is similar to that described from the early Desmoinesian, but on a much larger scale. Although lycopsid-dominated peat swamps persisted into the early Permian in China, lycopsid-dominated communities disappeared from Euramerica peat swamps at the end of the Desmoinesian (Gastaldo et al., 1996). Conifers, which are upland plants adapted to drier and well-drained, oxidized environments, begin to invade the lowlands replacing the coal swamp vegetation (Lyons and Darrah, 1989).

Peat-accumulating swamps and surrounding clastic wetlands are thought to have consisted of distinct communities with taxa specialized to living in those environments (Phillips and Peppers, 1984; Phillips, et al., 1985; DiMichele and Phillips, 1995; DiMichele and Phillips, 1996a; DiMichele and Phillips, 1996b). The Williamson #3 deposit represents a unique deposit dominated by a diverse assemblage of medullosan seed-ferns and *Cordaites* (Appendix B, 1). Yet, the seed-fern foliage from this locality has never been intensively studied. Because the morphological and anatomical features distinguishing plants of various habitats are most prominent in the leaves (Esau, 1977), evaluation of the foliar anatomy of *Alethopteris* may help to constrain the habitat of the Williamson #3 Coal assemblage. The pteridosperm leaf *Alethopteris* is very common throughout the Pennsylvanian, especially in compression-impression assemblages that may derive from plant communities growing in drained mineral soils. An evaluation of the anatomical variation of *Alethopteris* will provide better insight into the landscape and climatic changes that occurred during Pennsylvanian in North American coal swamps.

This study has implication for global diversity studies (Raymond, 1996). Several studies exist describing anatomical features of pinnules from coal balls (Leisman, 1960; Baxter and Willhite, 1969; Reihman and Schabilion, 1976a; Reihman and Schabilion, 1976b; Mickle and Rothwell, 1982) but classification of most species within the genus *Alethopteris* is based on morphologic characteristics from compression/impression fossils. Wagner (1968) described twenty-nine species and four varieties of *Alethopteris* based on morphology. His study included specimens from the Upper Westphalian and

Stephanian of the British Isles and Spain as well as France, Germany, Czech Republic, Turkey, and North America. Scheihing and Pfefferkorn (1980) reviewed *Alethopteris* from a single North American locality and identified four morphogroups, which could have been placed in six traditional species. They attributed the gradational character of traits used to delineate *Alethopteris* species in compression/ impression deposits to the morphological variation of leaves which can vary with soil type, water availability, type and proximity of other plants, maturity, position on plant, and amount and intensity of sunlight (Scheihing and Pfefferkorn, 1980). Anatomical features of *Alethopteris* provide a more precise individuation of pteridosperm species. A study of *Alethopteris*, within a single locality will contribute to a better understanding of size and shape variation in *Alethopteris* species and help to determine diversity within this important group.

Alethopteris and other seed fern foliage genera (*Neuropteris*, *Mariopteris*, and *Neuralethopteris*) have been used to delineate floral zones in the Lower to Middle Pennsylvanian (Read and Mamay, 1964; Peppers, 1996). Therefore, the present investigation of *Alethopteris* species in permineralized assemblages has the potential to further refine the biostratigraphy of permineralized deposits from the Desmoinesian of Iowa. This is especially important since many of the coals from Iowa are poorly dated.

MATERIALS AND METHODS

Geologic Setting

The precise stratigraphic placement of the Williamson #3 coal deposit remains uncertain because no records exist giving detailed information concerning the stratigraphy of the seam from which the coal balls were collected. In addition, the Late Mississippian karstified surface served to localize Middle Pennsylvanian coal deposition in Iowa, increasing the complexity of correlation (Ravn, 1986).

Although the exact position is unclear, different studies analyzing palynology and macrofossils from both compression/impression samples and coal balls have narrowed the possible stratigraphic placements of the Williamson #3 coals (Brotzman, 1974; Ravn, 1979, 1986; Peppers, 1996; Klare, 1997; Lesnikowska and Willard, 1997). The abundance and diversity of cordaites pollen, *Florinites*, in the coals of the latest Atokan-earliest Desmoinesian Kalo Formation suggest that the Williamson #3 deposit belongs to the Kalo Formation (Raymond et al., 2001). The two major coals of this formation are: the Blackoak Coal, placed in the latest Atokan based on last occurrences of several miospores, the most notable being *Dictyotriletes bireticulatus*; and the Cliffland Coal, marking the beginning of the Desmoinesian (Ravn, 1986). Coal balls collected from both the Blackoak Coal (Lost Creek Mine) and the Cliffland Coal (Patik Mine) contain cordaitalean-dominated assemblages (Costanza and Lesnikowska, personal communication) supporting the idea that cordaitalean-dominated coal-ball deposits from Iowa are derived from the Kalo Formation. The Blackoak Coal was correlated with the Pope Creek Coal of Illinois based on palynology (Ravn, 1979; Peppers, 1996). Ravn (1981) correlated the overlying Cliffland Coal to the Rock Island Coal. It should be noted that many problems exist with classification and designation of stratigraphic units in the early to middle Pennsylvanian of the Mid-continent. Ravn (1986) reviewed these nomenclature problems in his Appendix II of Ravn, 1986.

Sample Material and Preparation

Primary materials for this study come from the Williamson #3 Mine in Lucas County, Iowa, and include the peels and slides made from cut coal balls. Many of the original coal balls are on loan to Texas A&M University from the Thompson-Darrah coal-ball collections of the Harvard University Botanical Museum. Some of the study material comes from a sample of one hundred previously uncut coal balls (HU

64660-64706; HU 64868-64868; HU 64871-64881) prepared for a paleoecological study of the Williamson #3 deposit (Raymond and Phillips, 1983; Ramond et al., 2001). The remainder of the Williamson #3 material comes from eighty-five previously cut coal balls (HU 64710- 64788; HU 64882 – HU64887) in the Thompson-Darrah collections of Harvard University Botanical Museum. Previously cut coal balls may contain a biased sample of the floral assemblage because coal balls with poorly preserved, hard to identify remains may be discarded, while those with rare, well-preserved fossils are generally saved. Phillips et al. (1985) noted a higher abundance of aerial debris in cut coal balls from museum collections. Nonetheless, previously cut coal balls can be beneficial in systematic studies.

In addition to the coal balls, previously made slides were used. Slides were made from parlodion peels of Williamson #3 and other Iowa coal balls in the 1930's and early 1940's under the direction of W.C. Darrah. These slides are also on loan from the Harvard University Botanical Museum.

Most coal balls were cut perpendicular to the bedding plane to reveal the vegetation occurring within that coal ball. After the initial cuts, further cuts were made to expose certain features of the seed fern foliage. Acetate peels of the cut surfaces were made following the methods outlined by Joy et al. (1956), and when needed, slides were made from peels using Canadian balsam as the mounting medium. It is important to note that much time and care is taken in the preparation of the coal balls themselves. They are extremely delicate and begin to oxidize after the initial cut. Epoxy was used to fill subsequent cracks that resulted from the peeling process.

Experimental Methods

Peels made from the Williamson #3 coal balls were mapped using the centimeter^2 grid technique of Phillips et al. (1977). On each peel, the areas that contained seed-fern vegetation were documented, which helped to establish how the leaves changed through a set of serial peels of the same surface. When possible, measurements were made only on leaves sectioned perpendicular to the midrib. Round features such as secretory cells or bundle sheaths in the lamina were used to identify leaves in cross-section. Pinnules in paradermal, or tangential, section in association with pinnules in cross-section were documented. Although sectioning pinnules in paradermal view to observe them in cross-sectional view

proved difficult, the repeated occurrence of the Williamson #3 morphotypes with these pinnules reaffirms their placement in the genus *Alethopteris.*

Peels were studied and imaged using a Sony 3CCD color video camera (Exwave HAD) attached to a Zeiss stemi 2000-C binocular microscope (Light Source: Zeiss KL 15000LCD). The software used for imaging and measurements was Image Pro Plus 3.0. Slides were studied on a Zeiss polarized light microscope and imaged using a SPOT cam version 3.2. Image Pro Plus 4.5 was the software used for imaging and measurements.

Alethopteris pinnules in the Williamson #3 deposit were evaluated using traits established by previous workers (Appendix C). Each of these studies focused on the anatomical features of pinnules in cross-sectional view, although several morphological characteristics of pinnules were described from the split surfaces of coal balls. Diagnostic features identified from previous works and as a result of this study used for measurements and description of anatomically preserved leaves are listed in Table 1.

Perhaps due to taphonomic processes (Raymond, et al., 2001a), well-preserved *Alethopteris* pinnules are relatively rare. Of the 185 Williamson #3 coal balls evaluated for this study, thirty contained well-preserved *Alethopteris* foliage. Of these thirty, fourteen contained pinnules sectioned perpendicular to the midrib. Most *Alethopteris* pinnules consist of resistant cells and tissues (epidermis, vascular bundle sheath extensions associated with secondary veins, and portions of the midrib) and lack diagnostically important tissues (vascular bundles and mesophyll). While these pinnules often can be assigned to species and morphotypes, they are too poorly preserved for use in the individuation of species. Accordingly, thirty-eight extremely well preserved pinnules (twenty-four cross-sections and fourteen paradermal sections) were used to describe the morphology and anatomy of *Alethopteris* from the Williamson #3 deposit. A total of 19 traits were documented for each pinnule in cross-section. Thirteen traits were used to document twelve leaves in paradermal view. Morphotype 1 is the focus of this study due to distinct traits separating it from other species and morphotypes of *Alethopteris*. Because morphotype 2 is much more variable, it will not be discussed in detail and is used herein to separate morphotype 1 from other seed-fern pinnules in the Williamson #3 Mine.

Table 1
Traits used to describe and measure the anatomical features of *Alethopteris*

TRAITS	**Measurements**	**Descriptions**
	Lamina thickness in the midrib region	Midrib vascular bundale development
	Width of midrib	Characteristics of abaxial margin
	Lamina thickness in the blade region	Characteristics of adaxial margin
	Width across the cross-section of the pinnule (width of pinnule tip to tip)	Description of trichomes
	Epidermal cells	Description of secretory cells
	Hypodermal cells	
	Trichomes	
	Secretory cells	

Scatter plots were used to compare pinnules from the Williamson #3 deposit based on: 1, midrib thickness and width 2, total pinnule width and midrib width 3, total pinnule width and midrib thickness, and 4, lamina thickness in the blade portion of the pinnule and total pinnule width. A two-tailed student's t-test was used to test for statistically significant differences. This type of t-test assumes that the variances of both ranges of data are unequal and is used to determine whether two sample means are equal. If the means differ significantly ($P < 0.05$), the two morphotypes represent two different populations. A variation of the student's t-test, designed to test the probability that a single specimen belongs to the sample population (Simpson et al., 1960), was used to test for statistically significant differences between Williamson #3 morphotypes and previously-described species of *Alethopteris.* In these analyses, we compared a single pinnule, based on the average dimensions of each previously described *Alethopteris* species, to the entire population of each Williamson #3 morphotype.

RESULTS

Introduction

The form-genus *Alethopteris* was first used in 1825 by Count Kaspar von Sternberg in "Versuch einer geognostisch-botanischer Darstellung der Flora der Vorwelt" and is recognized within the family *Alethopteridaceae* (Wagner, 1968). Wagner (1968) describes four other form-genera recognized within this family differentiated based on the general morphology of the pinnules, the type of nervation, and attachment of pinnule to rachis (decurrent or constricted base). *Lonchopteridium* and *Lonchopteris* both have decurrent bases with partly pseudomosed and fully anastomosed veins. *Neuralethopteris* has non-anastomosing veins with a decurrent to constricted base. *Macralethopteris* is characterized by large pinnules, decurrent to constricted base, and non-anastomosing veins bifurcating near the midrib. *Alethopteris* is characterized by pinnules with a decurrent base, prominent midrib, non-anastomosing lateral veins. Comparisons between the pinnules in the Williamson #3 deposit to those described in Wagner (1960) resulted in the identification of *Alethopteris* from the Williamson #3 (Fig. 5)

Leisman (1960) and Baxter and Willhite (1969) compared morphological and anatomical features of *Alethopteris*. Based on similarities in size, shape, and revolute margins of pinnules, coal ball specimens were assigned to species already described from compression/impression material (Baxter and Willhite, 1969).

Two morphotypes of *Alethopteris* from the Williamson #3 Mine

Description of Morphotype 1

Pinnules are small, averaging 5.6 mm long by 1.7 mm wide with a decurrent base, prominent midrib, and non-anastomosing lateral veins. In transverse section, pinnule lamina is significantly enrolled. The adaxial surface is smooth except for an indention above the midrib. This indentation is most pronounced in the lower one-half to two-thirds of the pinnule, becoming less pronounced towards the apex. The abaxial surface of the lamina is relatively smooth with no ridges formed from the secondary vein bundle sheath extensions (Fig. 6). The average thickness of the pinnule in the midrib area is 1069μm. The range of thickness for the pinnule blade is 325μm -503μm.

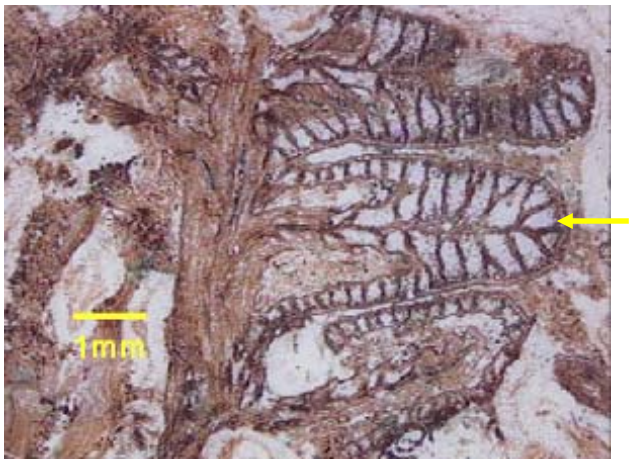


Fig. 5. Well-preserved paradermal section of a pinnule associated with cross-sectional views of morphotype 1 (HU 64864). Arrow indicates the midrib of the pinnule.

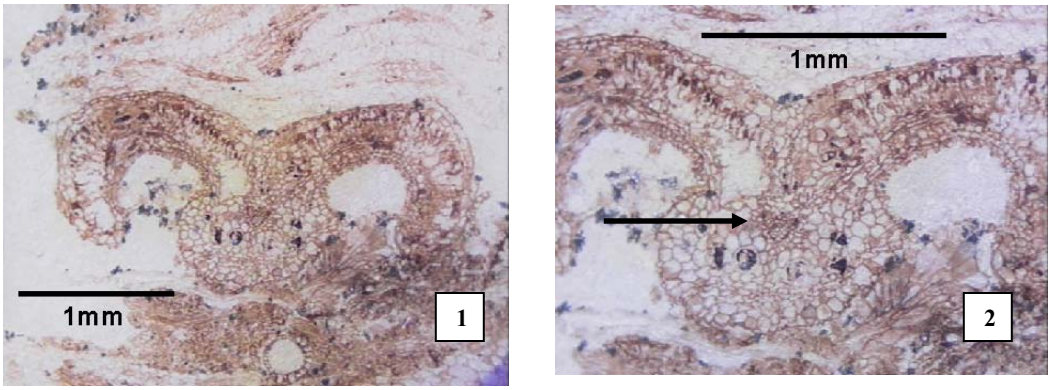


Fig. 6. Representatives of morphotype 1 in cross-sectional view. Key: (1) entire cross-section from lamina tip to lamina tip of morphotype 1; (2) pinnule from (1) magnified for a more detailed view. Arrow indicates the vascular bundle of the midrib.

The upper epidermis consists of small rectangular-shaped cells averaging 32μm x 46μm. Thick, cubic hypodermal cells averaging 64 μm x 66μm μunderlie the epidermal cells. Although the mesophyll is generally not well enough preserved to measure palisade and spongy parenchyma cells, the palisade layer appears to consist of long, closely spaced cells that occupy approximately one-third of the blade thickness. The spongy parenchyma cells, when preserved, are irregular in shape. The lower epidermal cells have approximately the same dimensions as the upper epidermis.

Although the midrib varies in shape and thickness from the base to tip of the pinnule, it is relatively large averaging 1201 μm in width across the thickest part (Fig. 6(1)). The ground tissue within the midrib consists of large, thin-walled parenchymatous cells with many secretory cells interspersed along the abaxial margin. These cells are generally filled with a black, resinous substance and average 107μm in length and 102μm in width. The vascular strand of the midrib is v-shaped and surrounded by large bundle sheath cells (Fig. 6 (2)).

Secondary veins within the blade portion of the pinnule are surrounded by a bundle sheath, but due to poor preservation the actual shape of the vascular strand could not be determined. Bundle sheath extensions extend up to the bottom of the hypodermal cells and to the top of the epidermal cells, but do not form ridges on the abaxial surface.

Trichomes, or leaf hairs, are prominent on the abaxial surface of the leaves. Unicelluar, papillate cells averaging 32μm in length and 27μm in width are associated with each lower epidermal cell. Multicellular, unicerate hairs are also present and average 146μm in length and 32μm in width. These trichomes can be up to 7 cells long, although some may have been longer. Glandular hairs have also been observed with a knoblike secretory swelling at the apex of the trichome (Fig. 7). Figure 7(4) shows a bulge forming off the midrib. This may represent the formation of a multicerate hair.

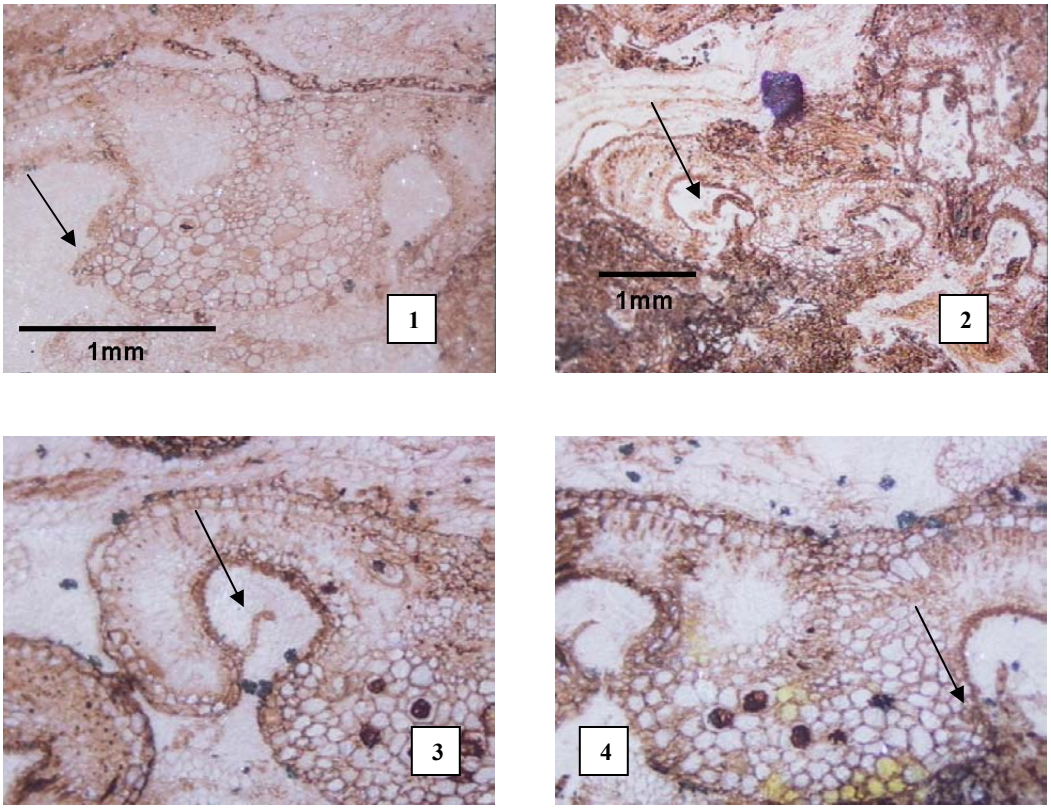


Fig. 7. Types of trichomes found on morphotype1. Key: (1, 2, 4) multiserate, multicelluar hairs; (3) uniserate, multicelluar hair with glandular tip.

Comparison of Morphotype 1 to Morphotype 2

The two common *Alethopteris* morphotypes present in the Williamson #3 deposit can be distinquished by differences in pinnule shape, pinnule thickness, and midrib size and shape (Fig. 8). Observed differences in hypodermal cell size, mid-rib dimensions, pinnule width, and blade thickness for each morphotype from the Williamson #3 were plotted to visually demonstrate that two distinctive morphotypes exist (Fig. 9, 10). In an attempt to expand on the idea that two morphotypes exist, a two-tailed student t-test was run comparing traits of morphotype 1 and morphotype 2 (Table 2). Results clearly show that two distinct populations exist for all but anticlinal hypodermal cells that were inconclusive. All other data resulted in P-values less than 0.05 implying a greater than 95% confidence that the two morphotypes represent two distinctive populations.

Morphotype 1 and morphotype 2 have similar total pinnule width and leaf thickness. They also share the characteristic of having papillate cells cover the abaxial surface of the leaf. They differ in the shape of the midrib. Morphotype 1 has a broad rectangular midrib that is wide especially in comparison to the thickness of the lamina at the midrib. The widest part of the midrib frequently occurs at the midrib-lamina junction. On the adaxial surface of the pinnule, the mid-rib is marked by a shallow depression in the lower one-half to two-thirds of the pinnule with no depression distially.

In comparison, on the abaxial surface of morphotype 2 the midrib has a rounded base. Distally, the widest part of the midrib is also at the midrib lamina. Proximally, the midrib is round and the widest part occurs well below the midrib-blade junction. On adaxial surface the midrib is marked by a deep furrow proximally that becomes distally shallow.

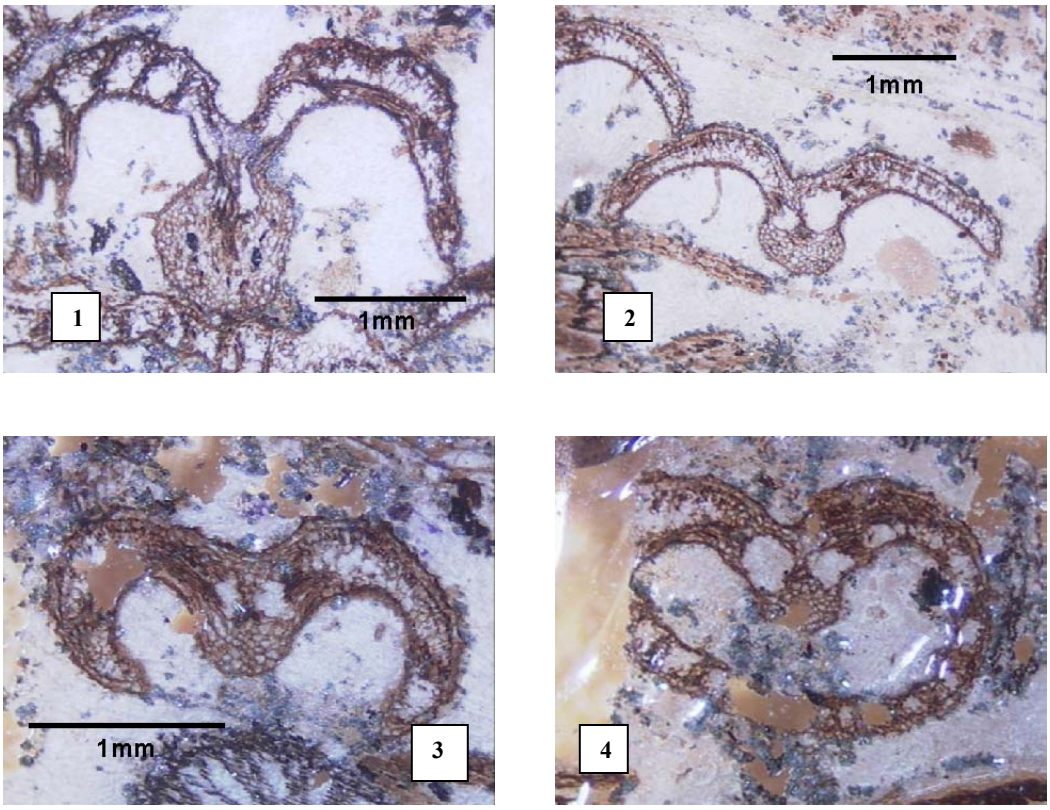
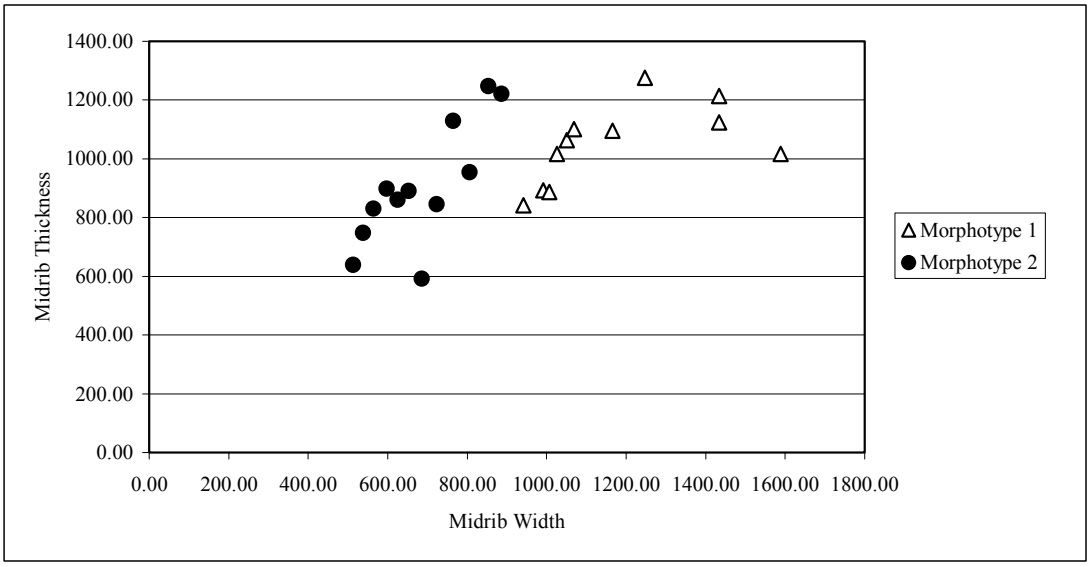


Fig. 8. Representatives of morphotype 2 in cross-sectional view. Key: (1) pinnule located near rachis; (2) pinnule from middle section of frond; (3) pinnule from distal section of frond; (4) pinnule near tip of frond.



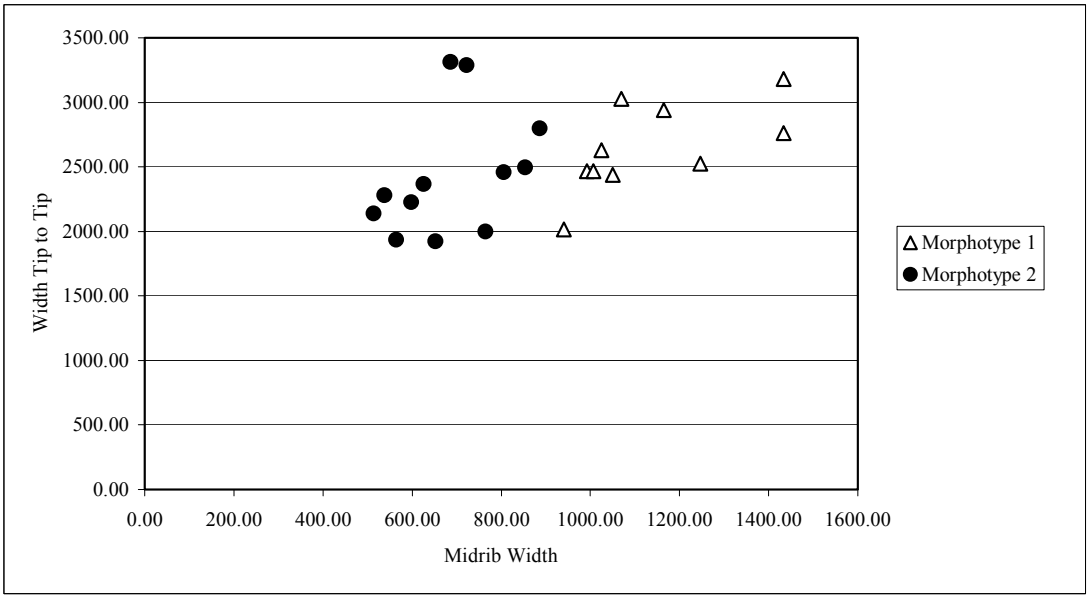
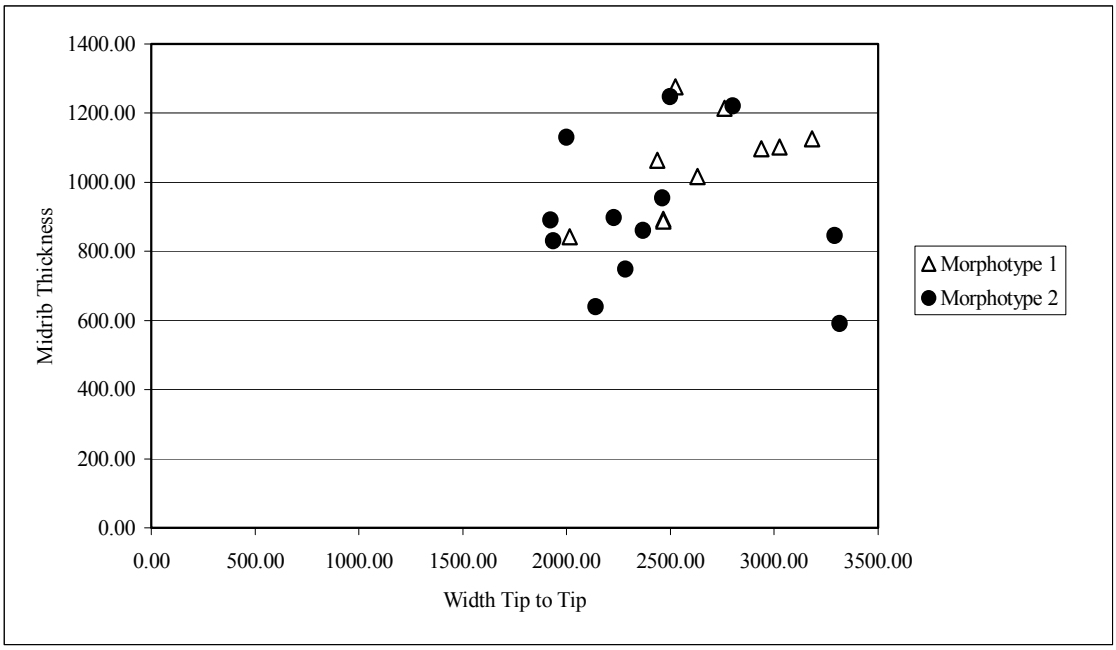


Fig. 9. Scatter plots comparing morphotype 1 to morphotype 2 based on midrib width versus width tip to tip and midrib thickness.



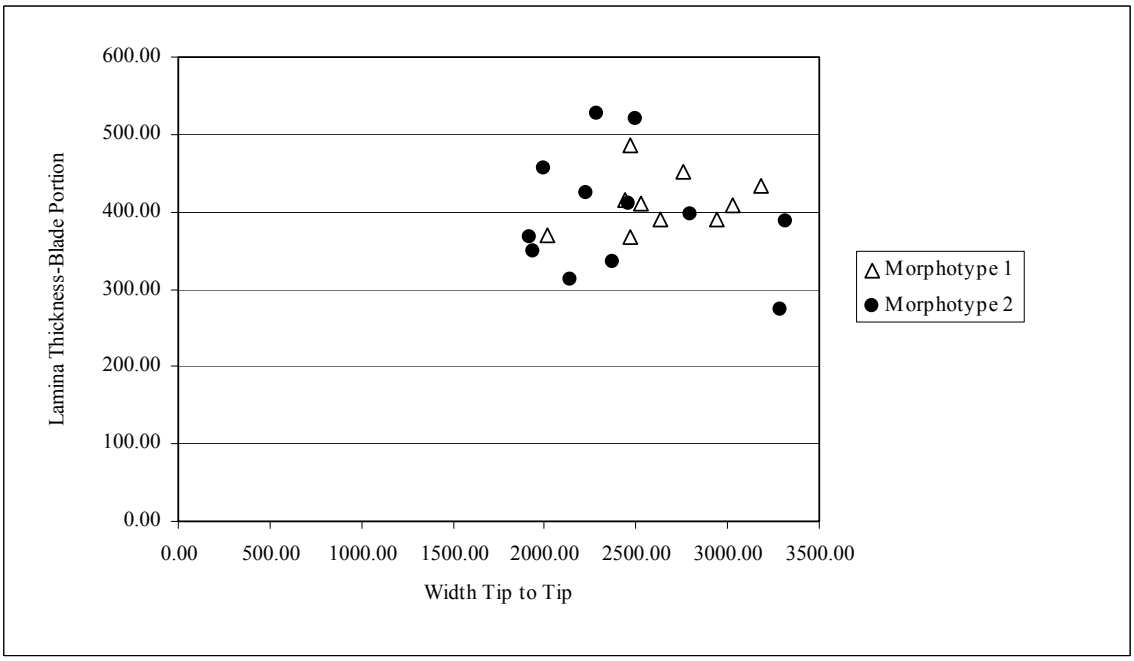


Fig. 10. Scatter plot comparing morphotype 1 to morphotype 2 based on width tip to tip versus lamina thickness at the blade portion and midrib thickness.

Table 2
Student t-test results for morphtype 1 versus morphotype 2.

Characterisitic	Calcualted t-value	P-Value
Lamina Thickness at Midrib	2.085962	0.021909
Midrib Width	2.131451	0.000012
Lamina Thickness Blade Portion	2.004044	0.022872
Anticlinal Epidermal Cells	2.007582	0.005270
Periclinal Epidermal Cells	2.006645	0.000054
Anticlinal Hypodermal Cells	2.001716	0.318363
Periclinal Hypodermal Cells	2.000997	0.031698

Comparison of Morphotype 1 to Named Alethopteris Species

Morphotype 1 is most similar to the previously-described species, *Alethopteris lesquereuxi.* Both are characterized by enrolled pinnule margins and the occurrence of multicellular hairs on the abaxial surface. *A. lesqueruexi*, however, differs in many respects. In *A. lesquereuxi*, the bundle sheath extensions associated with secondary veins in the leaf lamina extend from the hypodermis to below the lower epidermis, forming ridges on the abaxial side, giving the underside of the pinnule a bumpy appearance. Generally, in *A. lesquereuxi* the multicellular hairs only occur on the bottoms of these ridges and the bottom of the midrib; and no papillate hairs are present. The multicellular hairs of morphotype 1 occur on any part of the smooth abaxial surface, and the entire abaxial margin of the pinnule is covered with papillate hairs. Clearly, morphotype 1 represents a different population from published descriptions of *A. lesqueruexi* when lamina thickness at midrib and hypodermal cells are compared (Tables 3 and 4).

Table 3
Statistics run on *Alethopteris lesquereuxi* from Reihman and Schabilion, 1976. Key: (N) number of samples.

Characteristic	N	Published Mean (µm)	Sample Mean (µm)	Sample Std Dev.	Calc. t-value	Degrees of Freedom	Probablity
Lamina Thickness at Midrib	10	725	1068.9	124.1	2.64	9	0.95
Midrib Width	10	N/A	1201.2	214.7	5.33	9	N/A
Lamina Thickness Blade Portion	31	490	418.6	53.3	-1.32	30	0.8
Anticlinal Epidermal Cells	26	20	31.5	7.6	1.49	25	0.8
Periclinal Epidermal Cells	26	38	46.5	11.9	0.7	25	0.5
Anticlinal Hypodermal Cells	25	76	64	9.4	-1.25	24	0.7
Periclinal Hypodermal Cells	25	96	65.5	11.6	-2.57	24	0.98
Papillate Trichome Length (µm)	26	N/A	32.3	6.7	4.72	25	N/A
Papillate Trichome Width (µm)	26	N/A	27.3	4.1	6.48	25	N/A
Multicellular Length (µm)	9	272	145.8	81	-1.48	8	0.8
Multicellular Width (µm)	9	N/A	31.7	5.1	5.93	8	N/A

Table 4
Statistics run on *Alethopteris lesquereuxi* from Baxter and Willhite, 1969. Key: (N) number of samples.

Characteristic	N	Published Mean (µm)	Sample Mean (µm)	Sample Std Dev.	Calc. t-value	Degrees of Freedom	Probablity
Lamina Thickness at Midrib	10	735	1068.9	124.1	2.6	9	0.95
Midrib Width	10	N/A	1201.2	214.7	5.3	9	N/A
Lamina Thickness Blade Portion	31	150	418.6	53.3	5	30	0.99
Anticlinal Epidermal Cells	26	20	31.5	7.6	1.5	25	0.8
Periclinal Epidermal Cells	26	50	46.5	11.9	-0.3	25	0.2
Anticlinal Hypodermal Cells	25	100	64	9.4	-3.8	24	0.99
Periclinal Hypodermal Cells	25	140	65.5	11.6	-6.3	24	0.99
Papillate Trichome Length (µm)	26	N/A	32.3	6.7	4.7	25	N/A
Papillate Trichome Width (µm)	26	N/A	27.3	4.1	6.5	25	N/A
Multicellular Length (µm)	9	N/A	145.8	81	1.7	8	N/A
Multicellular Width (µm)	9	N/A	31.7	5.1	5.9	8	N/A

Mickle and Rothwell (1982) informally placed the anatomically-preserved *Alethopteris* pinnules from the Duquesne coal in the *A. serlii* morphogroup of Scheihing and Pfefferkorn (1982). Like morphotype 1, this pinnule has a relatively narrow blade. It differs from morphotype 1 in the shape of the vascular bundle in the midrib, lack of secretory cells, and the size and shape of midrib. *A. serlii* has a significantly smaller midrib that is round, whereas morphotype 1 has a broad, squarer midrib.

A.sullivanti when the characteristics of lamina thickness blade portion and hypodermal cells are compared (Table5, 6). Also, *A. sullivanti* has a much broader, narrow pinnule. The differences between morphotype 1 and *A. sulllivanti* is greatest when comparing the pinnule thickness at the midrib versus pinnule width tip to tip.

Table 5
Statistics run on *Callipteridium sullivanti* from Leisman, 1960. Key: (N) number of samples.

Characteristic	N	Published Mean (μm)	Sample Mean (μm)	Sample Std Dev.	Calc. t-value	Degrees of Freedom	Probablity
Lamina Thickness at Midrib	10	1445	1068.9	124.1	-2.9	9	0.98
Midrib Width	10	N/A	1201.2	214.7	5.3	9	N/A
Lamina Thickness Blade Portion	31	635	418.6	53.3	-4	30	0.99
Anticlinal Epidermal Cells	26	19	31.5	7.6	1.6	25	0.8
Periclinal Epidermal Cells	26	31	46.5	11.9	1.3	25	0.7
Anticlinal Hypodermal Cells	25	43	64	9.4	2.2	24	0.95
Periclinal Hypodermal Cells	25	43	65.5	11.6	1.9	24	0.9
Papillate Trichome Length (μm)	26	N/A	32.3	6.7	4.7	25	N/A
Papillate Trichome Width (μm)	26	N/A	27.3	4.1	6.5	25	N/A
Multicellular Length (μm)	9	N/A	145.8	81	1.7	8	N/A
Multicellular Width (μm)	9	N/A	31.7	5.1	5.9	8	N/A

Table 6
Statistics run on *Alethopteris sullivanti* from Reihman and Schabilion, 1976. Key: (N) number of samples.

Characteristic	N	Published Mean (µm)	Sample Mean (µm)	Sample Std Dev.	Calc. t-value	Degrees of Freedom	Probablity
Lamina Thickness at Midrib	10	888	1068.9	124.1	1.4	9	0.8
Midrib Width	10	N/A	1201.2	214.7	5.3	9	N/A
Lamina Thickness Blade Portion	31	537	418.6	53.3	-2.2	30	0.95
Anticlinal Epidermal Cells	26	19	31.5	7.6	1.6	25	0.8
Periclinal Epidermal Cells	26	25	46.5	11.9	1.8	25	0.9
Anticlinal Hypodermal Cells	25	41	64	9.4	2.4	24	0.95
Periclinal Hypodermal Cells	25	39	65.5	11.6	2.2	24	0.95
Papillate Trichome Length (µm)	26	N/A	32.3	6.7	4.7	25	N/A
Papillate Trichome Width (µm)	26	N/A	27.3	4.1	6.5	25	N/A
Multicellular Length (µm)	9	N/A	145.8	81	1.7	8	N/A
Multicellular Width (µm)	9	N/A	31.7	5.1	5.9	8	N/A

DISCUSSION AND CONCLUSIONS

A diverse assemblage of gymnosperms dominates the late Atokan-early Desmoinesian Williamson #3 deposit with pteridosperms contributing approximately thirty-five percent of the biomass. A distinct, anatomically preserved pteridosperm pinnule, morphotype 1, is presently described representing a probable new species of *Alethopteris*.

Morphotype 1 is most similar to the *A. lesquereuxi*. Both are relatively narrow pinnules with an enrolled margin. However, morphotype 1 has a significantly larger midrib, a narrower lamina, and more leaf hairs on the abaxial surface of the pinnule. In addition, papillate hairs cover the smooth abaxial surface of morphotype 1 with the occasional multicellular hair on the lamina or midrib. *A. lesquereuxi* lacks papillate hairs with multicellular hairs occurring only on ridges formed on the abaxial surface by the midrib and bundle sheath extensions extending below the lower epidermis. Both *A.serlii* and *A. sullivanti* have papillate hairs and trichomes on the abaxial surface, but differ in their lamina thickness at the midrib and lamina thickness in the blade portion. Also both are characterized by smaller hypodermal cells and less frequently occurring secretory cells.

A number of characters of morphotype 1 suggest adaptations for water-stress (xeromorphy) including leaf hairs, enrolled margins, the presence of a hypoderm, and a thick lamina contributing to a low surface to volume ratio. Because of the difficulty of maintaining roots in water-logged soils, swamp plants frequently display xeromorphic adaptations (Lambers et al., 1998). Morphotype 1 anatomically appears to be more extreme in its xeromorphic features, especially in comparison to other described species of *Alethopteris* from peat swamps. However, in appears unlikely that pinnules from the Williamson #3 Mine experienced seasonally dry condition on a regular basis because of its proximity to the Pennsylvanian paleoequator.

The plants found in association with morphotype 1 and morpotype 2 also suggests that these swamps experienced drier condition than the lycopsid-dominated swamps of the middle to late Desmoinesian. The presence of significant percentages of bisaccate conifer pollen (Cutlip, personal communicaton) and the dominance of cordaites and tree-fern/seed-fern communities indicate that local and

regional climate was drier during the deposition of the Williamson #3 coal. No conifer macrofossils have been recovered from the Williamson #3 deposit; thus, pollen probably derives from conifer communities growing outside the swamp. Both the anatomical characters of morphotype 1 and the other vegetational types found in the Williamson #3 deposit indicate the uniqueness of this deposit. Therefore, Late Atokan-early Desmoinesian gymnosperm-dominated peats record intervals of seasonally stressed conditions in the peat-accumulating swamps.

Finally, another difficulty in Carboniferous paleobotany is determining species-level relationships among pteridosperms. Although vegetative organs and seeds commonly occur together in assemblages, their fragmentary nature makes it difficult to interpret their taxonomic classification, placement and function in life. Conversely, coalified compressions are commonly found in sandstones and shales and reflect preservation of plants growing in clastic wetlands (DiMichele and Phillips, 1995). Pteridosperms dominated these mineral-rich deposits during the Middle Pennsylvanian and appear to have been better adapted to higher nutrient levels and an absence of standing water year round (Phillips, 1981; Pfefferkorn and Thomson, 1982; Gastaldo, 1987). As a result, the reported diversity and abundance of pteridosperms in coal ball assemblages is much less than in compression /impression assemblages (Phillips, 1981; Behrensmeyer and Hook, 1992).

This analysis introduces interesting data on the paleoecology of an Iowa swamp, but has disconcerting ramifications for diversity studies. Scheihing and Pfefferkorn (1982) demonstrated the gradational nature of many compression-impression characters and correctly grouped *Alethopteris* compression/impression species from their locality into morphogroups. At the same time, one conclusion of their study was that morphological characters alone might never reveal the biological species diversity of *Alethopteris* or any other pteridosperm foliage genus. Additionally, a single compression/impression species can encompass many anatomically distinct species. While both morphology and anatomical studies contribute to the understanding of species-level relationships, studies focusing on anatomical characteristics provide a more detailed analysis for the determination of diversity and paleoecology.

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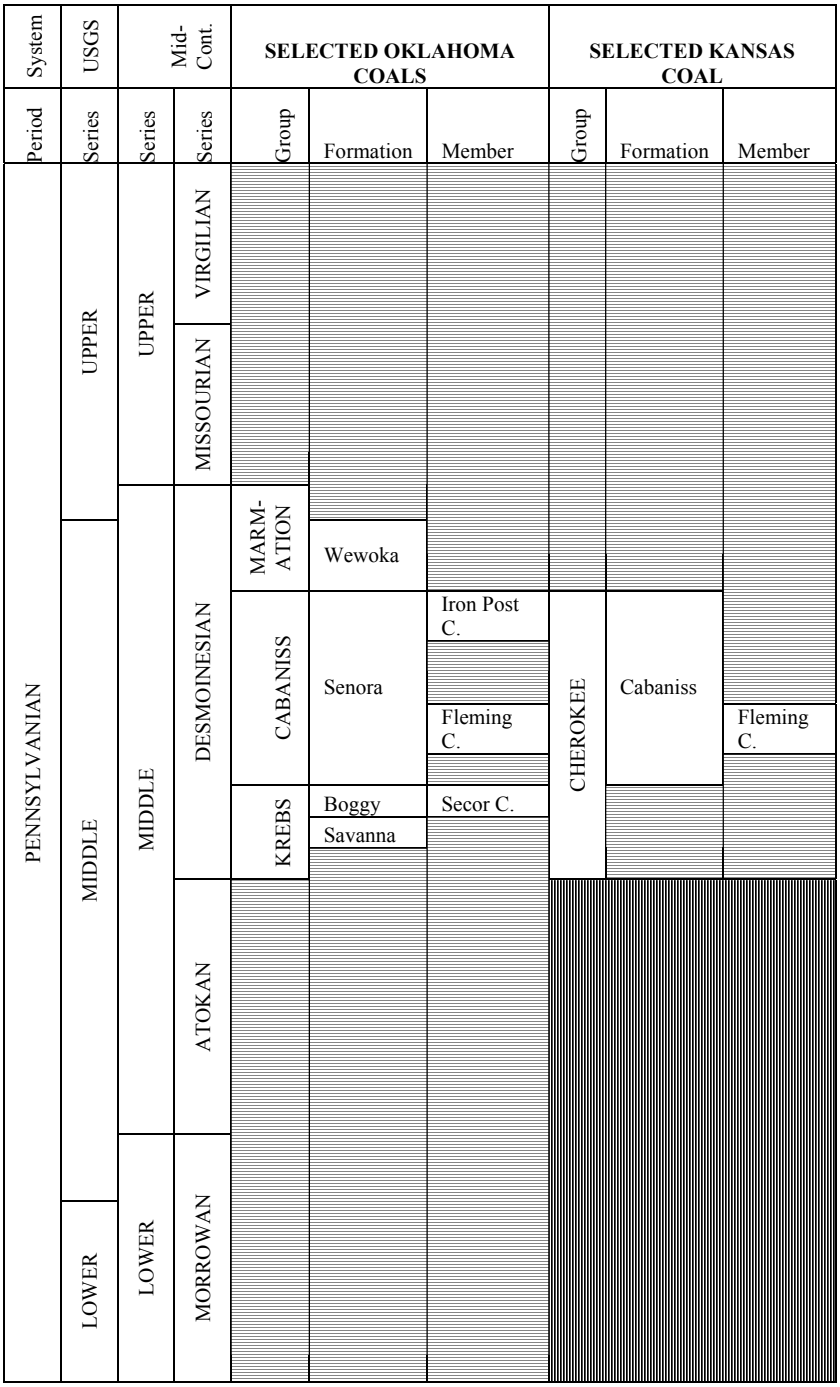
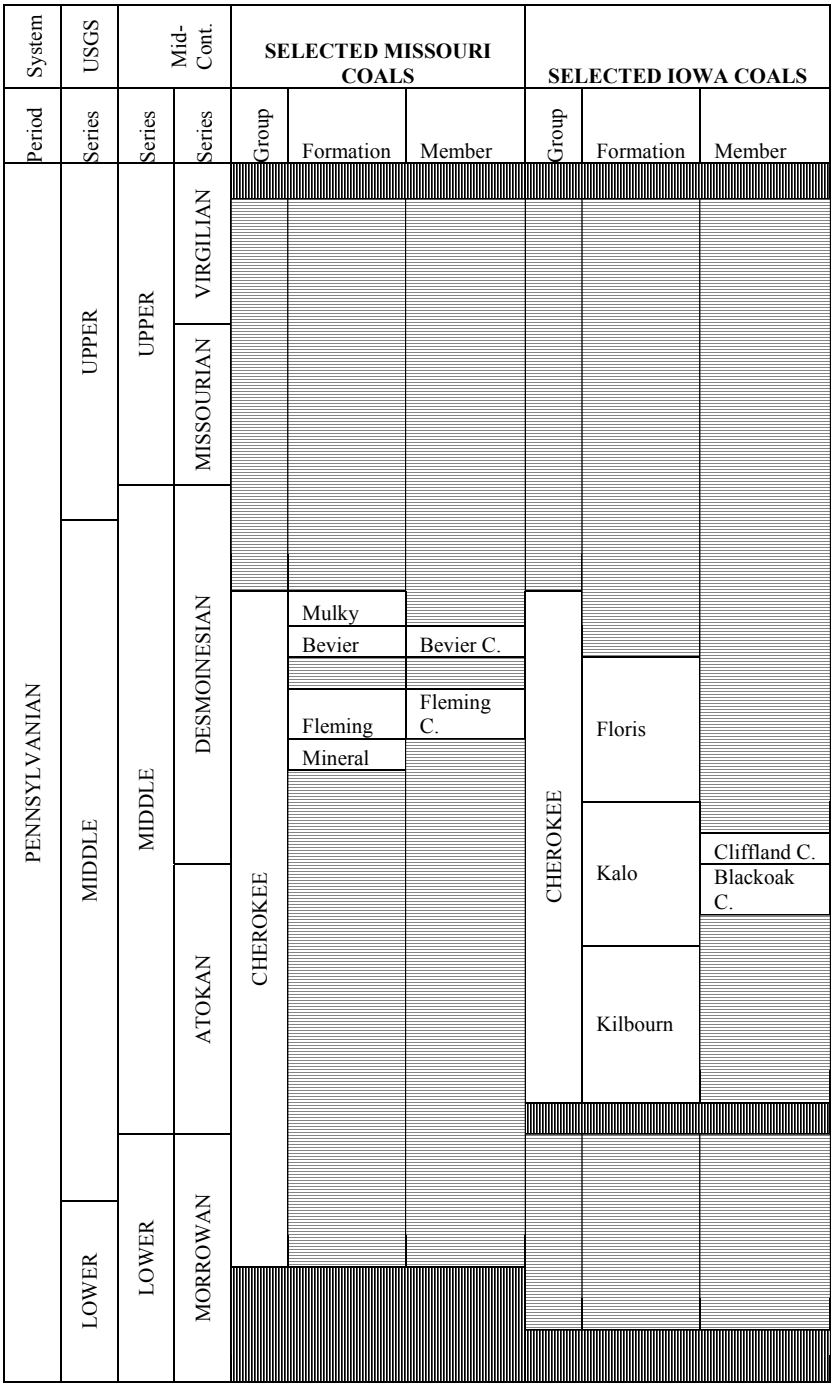
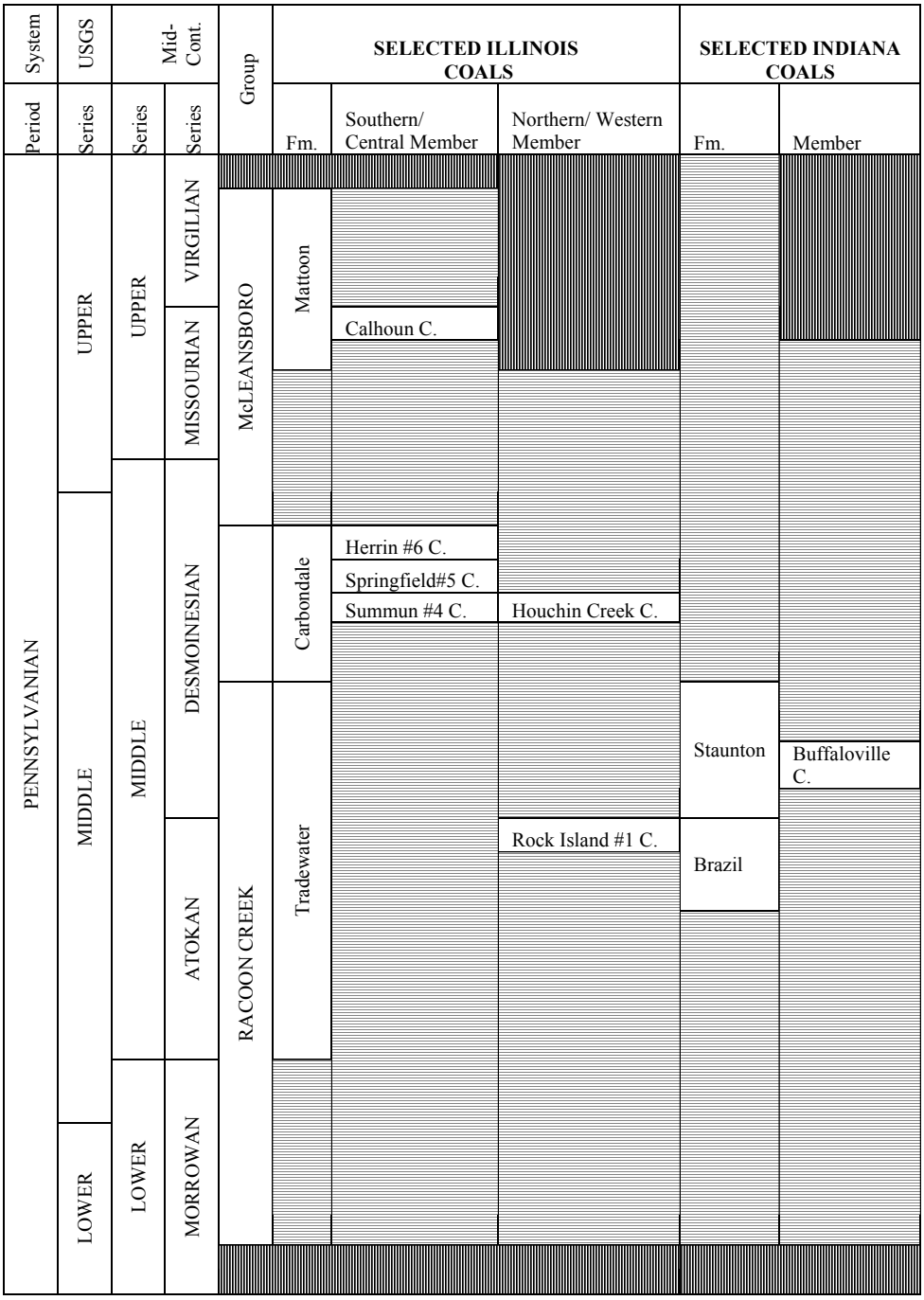
APPENDIX A



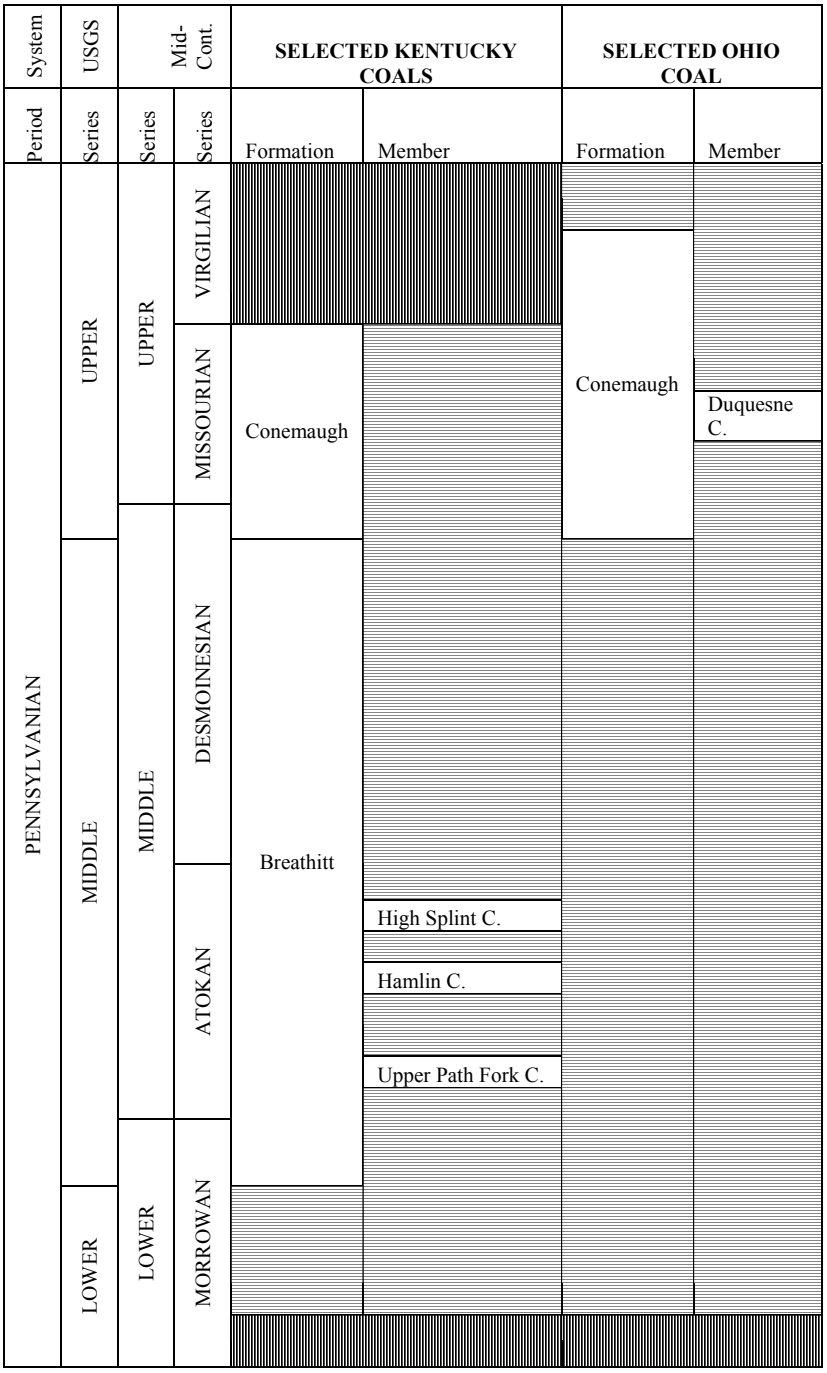
1. The stratigraphic position of selected coals from Oklahoma and Kansas deposited in the Western Interior Basin. Modified from Phillips (1980), Phillips et al. (1985), and Peppers (1996).



2. The stratigraphic position of selected coals from Missouri and Iowa deposited in the Western Interior Coal Province. Modified from Phillips (1980), Phillips et al. (1985), and Peppers (1996).

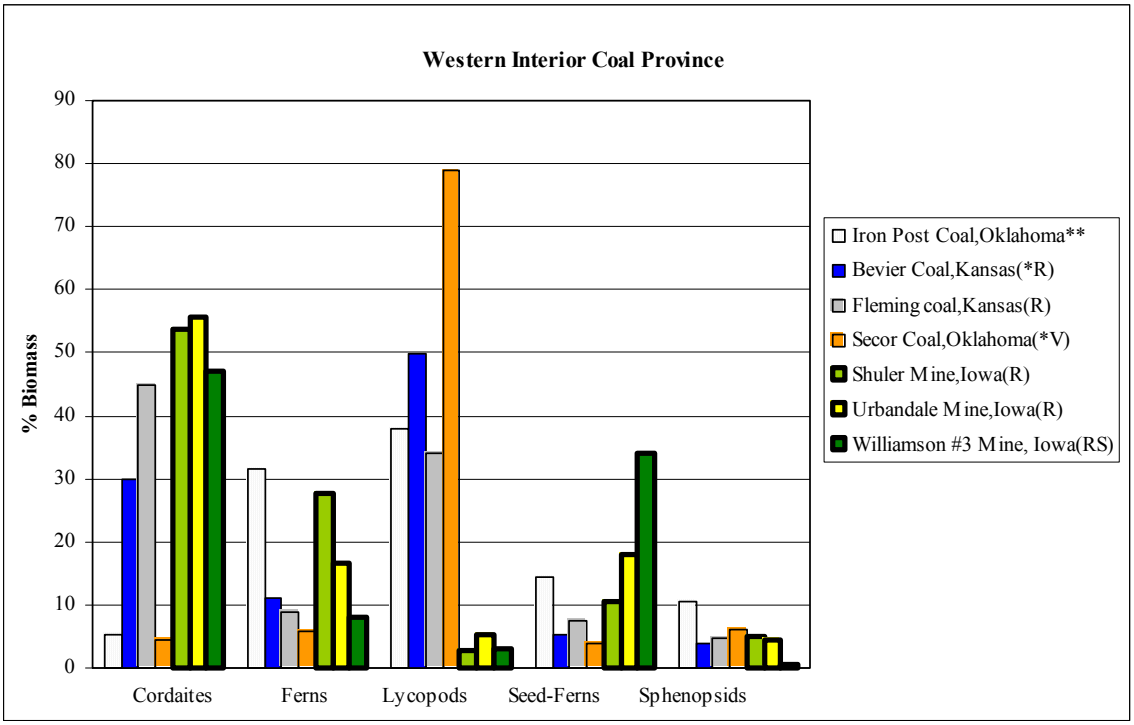


3. The stratigraphic position of selected coals from Illinois and Indiana deposited in the Illinois Basin. Modified from Phillips (1980), Phillips et al. (1985), and Peppers (1996).

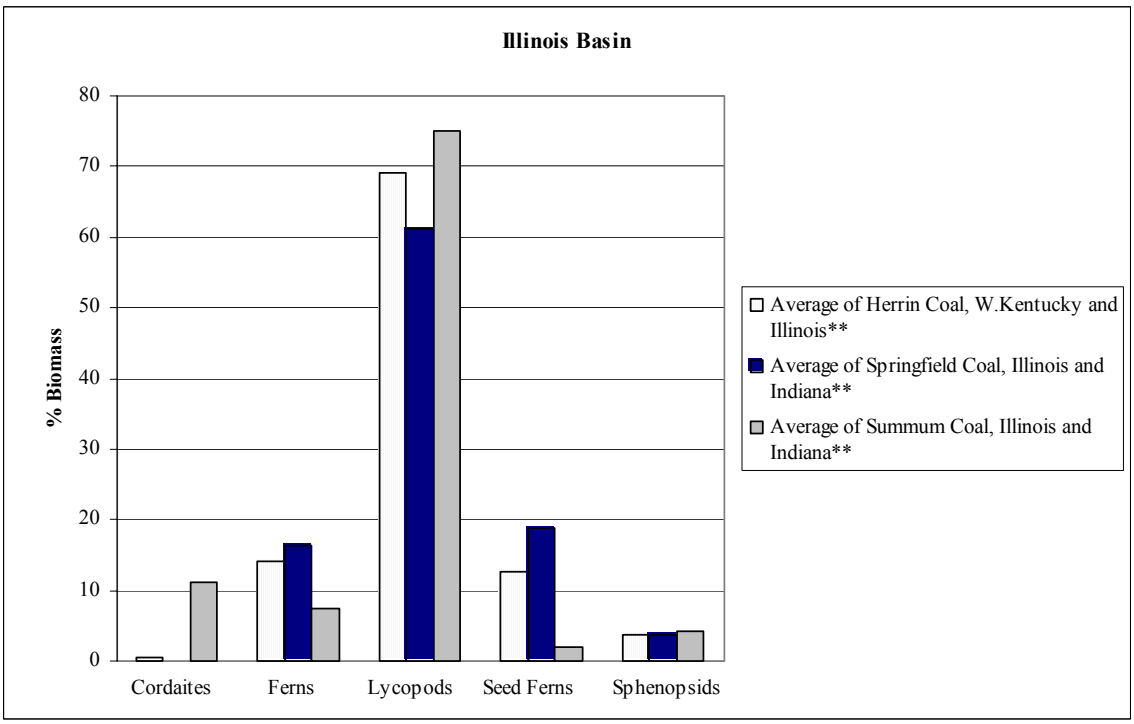


4. The stratigraphic position of selected coals from Kentucky and Ohio deposited in the Appalachian Coal Region. Modified from Phillips (1980), Phillips et al. (1985), and Peppers (1996).

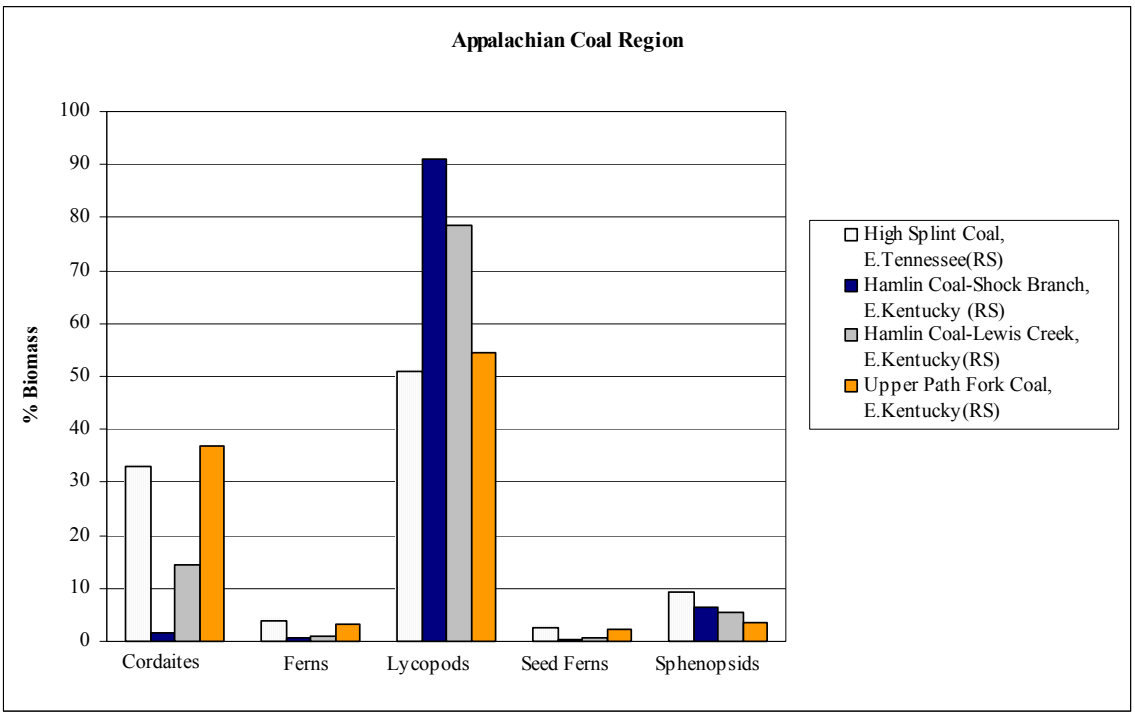
APPENDIX B



1. Percent biomass of coals and mines occurring in the Western Interior Province from youngest (Iron Post Coal) to oldest (deposits from the Iowa). Percent biomass from Iowa mines illustrated with a heavier border. Data modified from Phillips et al. (1985).
Key: (RS) random samples; (**) average percent biomass of both random samples and profiles of coal ball peat; (*R) average percent biomass from random samples; (*V) average percent biomass from profiles of coal ball peat.



2. Percent biomass of coals occurring in the Illinois Basin in order from youngest (Herrin Coal) to oldest (Summum Coal). Data modified from Phillips et al. (1985).
Key: (**) average percent biomass of both random samples and profiles of coal ball peat.



3. Percent biomass of coals occurring in the Appalachian Coal Region in order from youngest (High Split Coal) to oldest (Upper Path Fork Coal). Data modified from Phillips et al. (1985).
Key: (RS) random samples

APPENDIX C

Taxon	Coal and/or Coal Mine	Equivalent Coal/Stratigraphic Placement	Characteristics Abaxial Margin	Characteristics Adaxial Margin	Tricome Description	Authors
Alethopteris lesquereuxi	Fleming Coal, southeast Kansas	Cabaniss Formation, Cherokee Group, Desmoinesian Stage	abundant hairs on midrib, veinlet ridges, near revolute pinnule margins, and from lower epidermis		uniserate, multicellular; papillate cells absent	Baxter and Willhite, 1969
	Lovilia Mine, southcentral Iowa	equivalent to the Summon #4 coal of Illinois and the Bevier coal of Kansas	two rows of sclerenchyma cells occur in midrib, hairs on midrib, abaxial ridges, and on rachis	2 -3 rows of hypodermal cells in midrib region	large multicellular hairs	Reihman and Schabilion, 1976

Taxon	Coal and/or Coal Mine	Lamina Thickness at Midrib	Lamina Thickness-Blade Portion	Average Epidermal Cell (anticlinal)	Average Epidermal Cell (periclinal)	Average Hypodermal Cell (anticlinal)	Average Hypodermal Cell (periclinal)	Authors
Alethopteris lesquereuxi	Fleming Coal, southeast Kansas	720 - 750µm	tapers to 150µm at blade tips	20µm	50µm	100µm	140µm	Baxter and Willhite, 1969
	Lovilia Mine, southcentral Iowa	725µm	490µm	20µm	50µm	76µm	96µm	Reihman and Schabilion, 1976

1. Traits used by previous authors to described *Alethopteris lesquereuxi*.

Taxon	Coal and/or Coal Mine	Equivalent Coal/Stratigraphic Placement	Characteristics Abaxial Margin	Characteristics Adaxial Margin	Tricome Description	Secretory Canal Description	Authors
Callipteridium sullivanti	Fleming Coal (SW of West Mineral, KS); What Cheer Clay Products Mine,What Cheer, Iowa	Kansas: Fleming C., Cherokee Shale, Des Moines series Iowa: exact stratum unk. Des Moines series	most lower epidermal cells with one papillate hair		papillate cells; multicellular hairs up to 725µm in length; dark inter-cellular deposits suggest secretory function	scattered throughout ground tissue of rachis; frequently filled with dark-staining deposits probably representing secreted gums or resins	Leisman, 1960
Alethopteris sullivanti	Lovilia Mine, southcentral Iowa	approx. equivalent to the Summum #4 coal of Illinois and the Bevier coal of KS	multicellular hairs; numerous papillate hairs; cresent-shaped band of sclerenchyma 2-3 cells thick borders margin of midrib	no trichomes; sclerencyma, square-shaped, 4 cells thick borders margin in midrib	no papillae on lower surface of midrib; papillae cover lower epidermis also occasional multicellular hairs	often present on rachis	Reihman and Schabilion, 1976

Taxon	Coal and/or Coal Mine	Lamina Thickness at Midrib	Lamina Thickness-Blade Portion	Average Epidermal Cell (anticlinal)	Average Epidermal Cell (periclinal)	Average Hypodermal Cell (anticlinal)	Average Hypodermal Cell (periclinal)	Authors
Callipteridium sullivanti	Fleming Coal ; What Cheer Clay Products Mine at What Cheer, Iowa	max: 1445µm	max: 635µm	19µm	31µm	43µm	43µm	Leisman, 1960
Alethopteris sullivanti	Lovilia Mine, southcentral Iowa	888µm	537µm	19µm	25µm	41µm	39µm	Reihman and Schabilion, 1976

2. Traits used by previous authors to described *Alethopteris sullivanti*.

Taxon	Coal and/or Coal Mine	Equivalent Coal/Stratigraphic Placement	Characteristics Abaxial Margin	Characteristics Adaxial Margin	Tricome Description	Secretory Canal Description	Authors
similar to *A. pennsylvanica* Lesq. var. *pennsylvanica* , *Alethopteris zeilleri* Ragot, *Alethopteris grandinii* (Brong.) Goepp., *Alethopteris sarana* Guthorl, *Alethopteris barruelensis*	Duquesne Coal of the Conemaugh Group (near Steubenville, Ohio)	Late Pennsylvanian	multicellular and papillate hairs; single resin canal	occasionally hair bases on cuticular macerated cuticular fragments	papillate and multi-cellular; most hairs are broken or only hair bases are seen	traces and resin canals in the ground tissue of the midrib; single canal along abaxial margin	Mickle and Rothwell, 1982

Taxon	Coal and/or Coal Mine	Lamina Thickness at Midrib	Lamina Thickness-Blade Portion	Average Epidermal Cell (anticlinal)	Average Epidermal Cell (periclinal)	Average Hypodermal Cell (anticlinal)	Average Hypodermal Cell (periclinal)	Authors
similar to *A. pennsylvanica* Lesq. var. *pennsylvanica* , *Alethopteris zeilleri* Ragot, *Alethopteris grandinii* (Brong.) Goepp., *Alethopteris sarana* Guthorl, *Alethopteris barruelensis*	Duquesne Coal of the Conemaugh Group (near Steubenville, Ohio)	max: 600µm	300µ-400µm					Mickle and Rothwell, 1982

3. Traits used by Mickle and Rothwell (1982) to describe the *Alethopteris* from the Duquesne Coal.

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